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to designate the food requirement of a family of five, containing three children whose ages are between eight and sixteen. The diet provides 12,500 calories, contains 375 grams of protein, and cost one dollar and six cents per day in July, 1916. Of this, twenty-four per cent. was spent for bread, thirteen per cent. for milk, fifteen per cent. for meat, and the rest for seventy other articles. The bread ration contained 4500 calories or 35 per cent. of the total energy value of the food. This kind of information is of highest value to the housewife of limited means and can be successfully applied by any intelligent person.

"The Mothercraft Manual," by Miss Mary L. Read (Little, Brown and Company, 1916), presents, in language which is a delight, modern as well as old world knowledge helpful in the creation of the best environment for the family and describes the care, nutrition and development of the child.

GRAHAM LUSK

SPECIAL ARTICLES

THE THEORY OF SEX AS STATED IN TERMS OF RESULTS OF STUDIES ON PIGEONS¹

At the 1911 meeting of this society, in Princeton, I first made known the fact that the sex of pigeons had been experimentally controlled by Professor Whitman. The main fact of method being briefly that from a family cross practically only males, and from a generic cross nearly all males, are produced; but if, by special means the birds of generic crosses are forced to excessive reproductive overwork then the earlier eggs of such a series produce mostly or only males, while the later eggs—from the end of the series—will produce mostly or only females. At the same time and place I made to this society a first report upon the nature of the results of my own studies upon the ova of some of these sex-controlled series. These results then indicated—to quote from the published abstract of that paper²—

¹ Paper read December 28, 1916, before the American Society of Zoologists (New York Meeting).

² SCIENCE, N. S., Vol. XXV., No. 899, pp. 462-463; March 22, 1912.

that eggs (yolks) of *smaller size, higher water-content and smaller energy-content* (i. e., fewer units of physiologically available energy) can be *correlated with maleness* in the offspring. That eggs (yolks) of *larger size, lower water-content and greater energy-content* can be *correlated with femaleness* in the offspring.

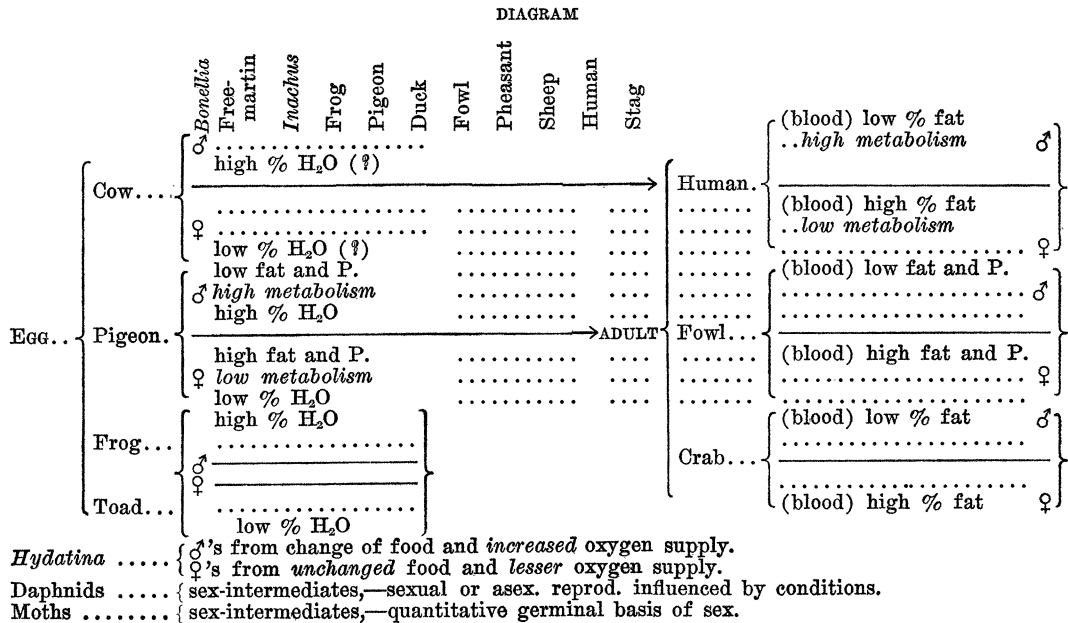
The later results, which I have from time to time presented before this society and elsewhere, have fully confirmed and much extended the evidence for that early announcement of the nature of the germinal differences which characterize the two sexes.

Though all of the several lines of study that I have carried out on the doves and pigeons have thrown light on the *nature* of germinal and adult sexual difference most of these lines of study were primarily designed to test the possibilities of selective fertilization, differential maturation and elective elimination of ova in the ovary as alternatives of a true sex-reversal or control. In view of the well-established fact that the hetero-gametic sex produces germs of two kinds—a sex-chromosome being a differential already recognized—it has seemed obligatory to supply decisive tests for the possibilities just named. This has all been thoroughly done in the pigeons; the result has been made possible because the female here is the hetero-gametic sex, producing male and female ova, and we have here learned to identify each of the two kinds. In these forms Whitman controlled sex and clearly demonstrated the methods of control. In these same forms I have for six years repeated the control and fully confirmed the method. In addition I have obtained adequate proof of the reality of the sex-control as against the above-mentioned alternatives and have further shown that in this material sex is a matter of essentially *all* gradations. And, of signal and unique importance is the fact that all, or at least many, gradations of sex are obtained from the same pairs of parents. The *outlines* of these findings have been published in several short papers beginning in 1911;³ the entire body of evidence

³ See under note 2; and, Carnegie Year Book, 1913; SCIENCE, Vol. 39, 1914; *Bull. Amer. Acad. of Med.*, Vol. XV., 1914; *Amer. Nat.*, Vol. L., July, 1916.

is now in course of preparation for publication. A still further fact of high importance has been learned from the pigeons, namely, that the sexual differences of the germs persist into the adult stages of the two sexes.

been a complete lack of corroborative evidence in other forms—the problem of the ultimate basis of sex was effectively broken loose from the morphological moorings which a decade of increasing knowledge of the sex-chromosomes



Again, since my first report of these results, several studies by other investigators on several different groups of animals, have appeared which in a most gratifying manner confirm the point of view of my first communication, and afford further evidence for the control and modifiability of sex.

It is the purpose of this paper to arrange some of the results of studies on the pigeon in a diagram, upon which are properly placed these various results of other investigators of sex, in order to show that we are already in possession of the skeleton of fact which is necessary for a theory of sex that accords with the most important fact of sex-reversal and control. And, that the theory of sex must be restated—or rather may now be stated—in terms that accord with the facts of sex-reversal is as certain as is the fact of sex-reversal itself. After our demonstration of the reality of sex-reversal in doves and pigeons—even there had

had, to a considerable extent, fastened it. For, at the same time that it was proved that our *experimental* conditions break the correlation which *normally* certainly does obtain between the chromosomal constitution of the zygote and the prospective sex of the adult, it was possible to identify those *functional* correlations which here continue to exist (as in the normal cases) and mark off the differences between the germs of prospectively different sex-value. We know, till now, of no other material in which this basal persistent function has been definitely identified and quantitatively measured in the germ. As I have elsewhere pointed out, the basic fact is that the two kinds of germs are differentiated by the degree or level of their metabolism. When either of these two kinds of germs is forced experimentally into the production of the opposite sex, the level of its metabolism is shifted to the level characteristic of the germs of that oppo-

site sex. While the chromosomal correlation is here forced to failure the metabolic correlation here persists. The chromosomal constitution is not an efficient cause of sex; it is but a sign or index⁴ and possibly an assistance in the *normal* maintenance of that which is essential—namely, two different metabolic levels. But the requisite metabolic level of the germ may be established in the absence of the usual or appropriate chromosome complex, and the sex of the offspring made to correspond to the acquired grade or level of metabolism.

These facts which we consider firmly established in the pigeons carry the further *essential* analysis of sex practically into the field of physiology and bio-chemistry. Further analysis of the basis of sexual difference—in germ or in adult—is to be sought in studies of the metabolic differences of the two kinds of sex-germs, of adults of the two sexes, and of individuals of intermediate sex. Now that the problem of sex has been shown to belong in the field of metabolism we shall be able to note, in connection with our diagram, that a number of the requisite data bearing on germinal and adult sexual differences are already at hand.

Turning now to the diagram we note that *egg* and *adult* stages are considered. In the egg of the pigeon we have identified maleness and femaleness by three differentials. Femaleness in the egg stage being accompanied by *low metabolism*, lower percentage of H₂O, and higher total fat and phosphorus, or of phosphatides. Maleness is here accompanied by *high metabolism*, higher percentage of water, and lower total fat and phosphatides. Now there are valid reasons for treating these three differentials not as absolutely separate and disconnected facts, but rather as aspects or corollaries of the same fact. For example, a *high metabolism* in a cell is consonant with less storage of fat and phosphatides, and with a more highly *hydrated* state of the cell-colloids. It follows that where data for either of

these three differentials are at hand, for either the germ or adult of any animal, we have in such data evidence of the kind we are looking for, *i. e.*, evidence for the association of a given type of metabolism with the germ or adult of a given sex.

TABLE I

Sexual Differences of Fat and Phosphorus in the Blood of Adult Fowls and Man

Sex	Av. Total Fat	Av. Total P.	Ratio P.
Males (roosters)	15.45	6.43	100
Non-laying females.....	17.87	7.42	115
Laying females	27.80	13.15	205
Males (man)	141.4		
Females (woman).....	226.0		

For what forms then are such data available? And, what is now known of the persistence of this definite type of differentiation of the two kinds of sex-germs into adult stages of the two sexes? Recently Lawrence and Riddle⁵ have shown that one of these differentials—or one aspect of *the* differential which my own work has demonstrated in the egg—is clearly continued in the *blood* of the adult male and female (see Table I.). Fowls were substituted for doves in this case in order to increase the size of the sample, and thus increase the accuracy of the analytical results. In birds, therefore, we have fairly clear evidence that the metabolic differences of male and female germs persist in the male and female adults. In mammals too these aspects of sexual differences of the adults have been fully demonstrated. Almost simultaneously with the above determinations, data were published by Goettler and Baker,⁶ which as we have pointed out, show that the blood of the human male contains less fat, that of the female more.⁷ Further, the *basal metabolism* of the human male and female has recently been accurately

⁴ Since the chromosomes are *structural* characters they can not be expected readily to *alter* their numbers, etc., in response to new quantitative levels attained (permanently) by the fundamental *cell-functions*.

⁵ "Sexual Differences in the Fat and Phosphorous Content of the Blood of Fowls," *Amer. Jour. of Phys.*, Vol. XLI., September, 1916.

⁶ *Jour. Biol. Chem.*, XXV., June, 1916.

⁷ This result seems to have been anticipated by Gorup-Besanez in 1878.

determined by Benedict and Emmes;⁸ they find that the metabolism of man is 5 per cent. to 6 per cent. higher than that of woman.

Have we any measure of either of our differentials in any mammalian egg? I think that the experiments on sex-determination in cattle, together with an observation by van der Stricht, afford some evidence that the water-content of the male-producing egg is high, and that of the female-producing egg is low. Thury reported in 1862 that from fertilizations made in the early period of heat in cattle an excess of females were produced; and that later (delayed) fertilizations give rise to an excess of males. Similar experiments have been four or five times repeated by others, and these have all shown an excess of one or the other sex in accordance with such early or late fertilization.⁹ No one definitely knows whether the ovum of the cow absorbs water in the Fallopian tubes in this interval between ovulation and fertilization, but we do know that every amphibian, reptilian and avian egg that has been investigated does absorb very appreciable amounts of water while being passed from the ovary to the exterior. And, van der Stricht has described phenomena of growth or swelling of the yoke granules in one mammal—the bat—which, I am sure from my own studies on yolk, indicate the taking up of water by the egg of this mammal. It is highly probable, therefore, that precisely that *time relation* which leads to an excess of males in cattle is preceded or accompanied by an increased hydration of the ovum. In mammals therefore there is some evidence that a shift of the metabolic level—as indicated by one partly known sex-differential—is associated with the observed changes in the sex-ratio of the germs which are thus modified. Further, in one adult mammal—man—two of the three sex-differentials have been definitely demonstrated. These results for both the egg and adult stages of the mammal are at every point in

⁸ *Jour. Biol. Chem.*, Vol. XX., 1915. These authors give references to earlier literature.

⁹ The use of the terms *early* and *late* fertilizations assumes that some ovulation occurs either immediately before, or shortly after, the beginning of heat.

complete agreement with our data for both the egg and adult stages of the bird.

Experiments on the frog and the toad have afforded evidence for the control of sex. This evidence by many is not thought conclusive. Though selective fertilization has been eliminated as a possibility by Kuschekewitch there remains the possibility of parthenogenetic development to account for the excessive male-production in his experiments with the frog. But this appeal makes it impossible to explain the great excess of *females* obtained by Dr. King on the eggs of the toad, and leaves such doubters to lean here upon the discredited staff of selective fertilization—a proposition wholly disproved for the related frog and for the pigeon.

How does this situation look in the light of the sex-differentials already noted for birds and mammals? Richard Hertwig,¹⁰ and later Kuschekewitch,¹¹ allowed frog's eggs to over-ripen—a process during which *the eggs take up water*—and obtained (in the case of the latter author) in some cases a total of 100 per cent. of males. Dr. King¹² did the converse of this experiment with toad's eggs—*withdrawing water* from them before fertilization—and obtained nearly or quite 90 per cent. of females in cases where the mortality was less than 7 per cent. According to our knowledge of the sex-differentials in the pigeon's eggs both of these experiments might have been predicted to result as these three investigators have reported.

In the spider-crabs Geoffrey Smith¹³ has shown that both the blood and the liver of the adult male crabs contain less fat than do the blood and liver of the females. Here once more the facts concerning one of the sex-differentials is in complete accord with all the preceding cases. In the parasitically castrated spider-crabs Smith and Robson were able to show, moreover, that *the parasitized male crabs, which under these conditions gradually assume several female morphological character-*

¹⁰ *Verhand. deutsch. zool. Gesellsch.*, 1906.

¹¹ *Festschrift. f. R. Hertwig*, 1910.

¹² *Jour. of Exp. Zool.*, Vol. 12, April, 1912.

¹³ *The Quart. Jour. of Micr. Sci.*, Vol. 57, November, 1911.

istics, are also found to have assumed the type of fat metabolism which characterizes the normal female crab. How much these facts contribute to, and how completely they adjust themselves to, our own general theory, will be realized only after a moment's reflection.

A glance at the diagram indicates three other groups of animals which experimental work has thrown into the general question of the control of sex. The information at hand for these forms does not so expressly concern the egg as does that from the preceding cases, but all of these latter groups are concerned with early stages—some of them with the generation preceding the egg whose sex seems influenced by conditions. The results of studies of the first of these groups—*Hydatina*—are of such a kind as to show that they are in general accord with the metabolic differentials of all of the previously mentioned cases of sex-control. One can scarcely doubt that *change* of food, and *increased oxygen* supply are consonant with increased metabolism, just as the studies of Whitney¹⁴ particularly, and later of Shull,¹⁵ have shown that these changes lead to the appearance of male-producing daughters.

The second of these groups—the Daphnids—have been studied by three independent investigators who agree upon two points that are of importance in the question of the control of sex, and to the general theory of sex as stated here, though the results throw little light on precisely what is causally involved. Issakowitch,¹⁶ Woltereck¹⁷ and Banta,¹⁸ all find numerous *sex-intermediates* in a material for which all agree that the type of reproduction—sexual or asexual—is influenced by environmental conditions. All further agree that “unfavorable conditions” (or is it a *change* from favorable conditions?) tends toward *sex-*

ual reproduction, while “favorable conditions” favor asexual reproduction.

In the third of these groups—the moths—the studies of Goldschmidt, and Goldschmidt and Poppelbaum,¹⁹ and the work of Machida, have demonstrated again sex-intermediates of various grades. Moreover, it has been shown that from among the various geographical races of moths certain matings can be arranged which produce rather definite types of male- or female-intermediates—or sex-intergrades, as Goldschmidt elects to call them. And further, from pairs involving still other species still other levels or grades of sex-intermediates may be freely obtained. A more or less factorial basis of the phenomena has hitherto been used in the discussion of these results; but recently Goldschmidt²⁰ has stated that “very important new facts will be published later which will probably enable us to replace the symbolistic Mendelian language, used here, by more definite physico-chemical conceptions.” Such newer descriptions—we would say—is wholly in line with the requirements of present data on sex. In Whitman's and our own material it has been clear from the first that the results far overstep the possibility of treating them in Mendelian terms, for it has been apparent from the beginning that we have had to do not with three or four *points* merely, but with a *flowing graduated line*. In the work with the moths, however, sex is clearly described in *quantitative* terms, and we can readily believe that when the functional basis of sex can there be identified, sex will be found to accord with metabolic grades there, as it does elsewhere.

It is clear then that all of the animal-forms for which there is reasonable evidence of sex-control show important correspondences with the situation fully elucidated in the pigeons. And that where the sex-differentials known to

¹⁴ SCIENCE, N. S., Vol. 39, June 5, pp. 832–33, 1914. Also *Jour. Exp. Zool.*, Vol. 17, November, 1914, and later papers.

¹⁵ Abstracts of Amer. Soc. Zool., December meeting, SCIENCE, N. S., Vol. 43, 1916.

¹⁶ *Biol. Centralbl.*, Vol. 25, 1905.

¹⁷ *Intern. Rev. d. gesamt. Hydrobiol. u. Hydrogr.*, Vol. 4, 1911–12.

¹⁸ Carnegie Year Book, 1915, and *Proc. Nat. Acad. Sci.*, Vol. 2, October, 1916.

¹⁹ Goldschmidt u. Poppelbaum, *Ztschr. induct. Abstammungsl.*, Vols. VII. (1912), and XII. (1914), and other papers 1913–16 by both authors. See R. Goldschmidt, below.

²⁰ R. Goldschmidt, *Amer. Nat.*, Vol. L., December, 1916.

exist in the pigeon's ova have been traced in adults of the two sexes, the parallel rigorously holds there also. A general classification of male and female adult animals on the basis of a higher metabolism for the one, and a lower for the other, was indeed made by Geddes and Thomson²¹ many years ago. There can now be little question that this conclusion of these authors is a correct and important one.

It remains to point out that another very old, and much-worked line of investigation supplies further confirmatory evidence for our present point of view. Studies on the effects of castration, gonad-transplantation, and gonad-extract injection, constitute a large body of observations which deal with sexual phenomena associated with the *internal secretions* of the sex-glands. These internal secretions, let it be remembered, are themselves *metabolites*, which have the capacity to *influence the metabolism* of some, many, or of all the tissues with which they came in contact, or which they may reach indirectly. A partial list of the animal forms that have been most studied in this respect is written vertically on the top of our diagram—in a position intermediate to egg and adult. The number of these animal forms might be much increased, and the names of the investigators of this aspect of the modification of sex are quite too numerous²² to be mentioned here.

²¹ "The Evolution of Sex," 1890, Humboldt Publ'g Co., New York.

²² The following partial references are suggested by the particular animals listed in the diagram: *Stag*—Darwin (1868); Caton (1881); Fowler (1894); Rörig (1900). *Human*—Hegar (1893); Selheim (1898); Hikmet and Renault (1906); C. Wallace (1907); Tandler and Gross (1909). *Sheep*—Shattock and Seligman (1904); Seligman (1906); Marshall and Hammond (1914). *Guinea-pig*—Bouin and Ancel (1903-09); Steinach (1910-13). *Pheasant*—Gurney (1888). *Fowl and Duck*—Darwin (1868); Gurney (1888); Foges (1903); Shattock and Seligman (1906-07); Goodale (1910-16). *Pigeon*—Riddle (1914). *Frog*—Nussbaum (1907); Pflüger (1907); Steinach (1910); G. Smith (1912). *Inachus and Carcinus*—Potts (1909); G. Smith (1910-12). *Free-martin*—Lillie (1916). *Bonellia*—Baltzer (1914).

But the present point of interest is that these results, as a whole, demonstrate that *the extent of sexual modification in the experimental animal is, in general, in proportion to the immaturity of the treated animal*. That is to say, the earlier the internal secretion of the gonad is supplied or withdrawn, the more profound is the sexual modification of the individual. The stag is a form that has long been known to show thus a considerable and beautiful series. The free-martin—another Ungulate—is now known to exemplify a much earlier point at which the foreign internal secretion begins to act; and here, true to the rule that has been established elsewhere in all this general line of work, the resulting modification is correspondingly strong and striking. When, by whatever means, we effect a change in the metabolism (which is the essential thing) at a still earlier stage—in the egg-stage, in our own and in some other experimental reversals of sex,—then we obtain individuals whose sexual nature is quite thoroughly reversed; in many cases completely so, and in still other cases with varying degrees of completeness.

Professor Whitman's main decisions concerning the *nature* of sex may here be briefly stated. These decisions were that the male proceeds from a "stronger" germ, has greater "developmental energy," and "carries the processes of development farther" than does the female. I am confident that his results fully justify his conclusions; and that these are in the completest harmony with the later and fuller developments of the sex-studies in the pigeons, and thus with the theory of sex which has been outlined in these pages.

In conclusion, our present definite knowledge of the metabolic basis of sexual difference, and the methods of attack which this new knowledge brings with it, offer the surest guarantees that the problem of sex can now be studied—and, indeed, the basal facts of the problem must be studied—in the field of the elemental protoplasmic functions.

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